

Hard Core or Soft Core: On the Characterization of Animal Space Use

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Abstract

The delineation of animal home ranges is a long studied topic where kernel density based methods have been widely employed. Moreover, certain methods have been traditionally utilized for characterizing animal core areas, though a robust method, spanning species and environments, is still needed. We present a new method for statistical core area estimation when available data are limited to temporally independent animal locations with continuous spatial support on a bounded region. A key concept to this method is the optimal partitioning of a clustered spatial point process into a set of two complete spatially random point processes such that the union of their support is equal to the home range. Additionally, we account for uncertainty in the core area delineation by allowing it to be a random set that is parameterized and estimated with Bayesian methods.

Key Words: Spatial Point Process, Complete Spatial Random, Clustering, Bayesian

1. Introduction

1.1 Background: Animal Space Use

Core areas are a frequently reported measure of animal space use and have been used to answer questions about a wide range of ecological topics such as social information transmission (Darden et al., 2008), interspecific competition (Neale and Sacks, 2001), trophic cascades (Prange and Gehrt, 2007), habitat selection (Chamberlin et al., 2003), reproductive success (Thompson et al., 2007), and territorial defense (Darden and Dabelsteen, 2008). Delineation of core areas might also be helpful for testing hypotheses about home range and body mass relationships (du Toit, 1990). Thus, the ability to accurately delineate core areas is of fundamental importance for answering many questions in ecology.

The first description of a core area is attributed to Kaufman (1962) who described a core area as being an area within the home range that “. . . is used more frequently than any other area, and that this area probably contains the principal home sites and refuges and the most dependable food sources.” Thus, any method developed to estimate core areas must precisely capture those areas of a home range that are used more heavily than would be expected by random space use patterns (Powell et al., 1997). Many techniques and rules-of-thumb have been proposed to delineate core areas and depend on the type of home range estimator used (e.g., Samuel et al., 1985; Samuel and Green, 1988; Seaman and Powell, 1990; Wray et al., 1992; Shivik et al., 1996; Hodder et al., 1998; Kenward et al., 2001; Barg et al., 2005). The majority of these methods, however, do not initially test for the existence of a core area (i.e., a spatial subset of the home range with higher intensity). This is problematic because these same techniques will generally estimate a core area, even if one does not exist (Powell 2000). The most common methods currently used to delineate home ranges and core areas rely on minimum convex polygons (Hayne, 1949) and kernel techniques (Worton, 1989; Laver and Kelly, 2008). The most common rule-of-thumb for these two techniques is to define the core area as the smallest boundary within which 50% of locations occur (convex polygon technique), or encompassing 50% of the density estimate (kernel technique; Laver and Kelly, 2008). But with every point pattern, random or clustered, these decision rules can estimate a “core area” (Powell, 2000). This is problematic because it can allow for misleading results and interpretation of space use patterns.

Assuming that an individual exhibits a clustered point pattern, most current methods rely on subjective rules having no biological significance as it relates to core areas. Even within a species, there is no consensus as to the best method to delineate core areas. For example, researchers of coyotes (*Canis latrans*) using kernel methods have used isopleths varying from 30-65% to define core areas (e.g., Shivik et al. 1996, Arjo and Pletscher 1999, Bromley and Gese 2001, Neale and Sacks 2001, Thornton et al. 2004, Young et al. 2006). Nearly all of the studies using kernel methods reviewed by Laver and Kelly (2008) defined core areas with the 50% isopleth. While many of the studies likely capture the core area, they may do it imprecisely, capturing a large area that is actually non-core area. For example, if the 15% isopleth captured all of the clustering in the point pattern for a given individual, delineating a core by the 50% isopleth would also capture the core area, but overestimate its size. Similarly, it might also be possible that the core is best captured by an isopleth $> 50\%$, but if the 50% isopleth is used, the core area will be underestimated.

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By defining core areas with the same rules-of-thumb (e.g., 50% isopleth) across studies, it implies that core areas are functionally the same across species, social classes, temporally, etc. Is it really valid to assume that all of these groups will show the same clustered spatial patterns within their home ranges? For example, would we expect the core area of a nesting bird species to be described by the same rules as a whale? The bird's core area would likely represent nesting activity, whereas the whale's might represent areas of abundant forage. Similarly, would we expect the female of that bird species, which is obligated to incubate, to have the same clustered spatial pattern as the male which spends the majority of its time hunting, and only briefly returns to the nest to deliver prey? In both of these examples, the functional significance of a core area is likely different between the groups, and should, thus, be described for those specific individuals based on their ecology and not on convention.

A few methods have been proposed that attempt to address these problems (e.g., Samuel et al., 1985; Seaman and Powell, 1990; Kenward et al., 2001). Each of these methods attempts to delineate core areas based on the individual rather than arbitrary rules, however, they differ in their abilities to accomplish this task and to test if there is clustering in the point pattern. The method presented by Samuel et al. (1985) relies on chi-square tests for spatial clustering, which requires a relatively large number of observations, due to the requirements of minimum cell values for chi-square tests (Kenward et al., 2001). This method also is limited in its ability to define cores for only clustered point patterns (Powell, 2000). The Area Independent Method (Seaman and Powell, 1990) attempts to delineate core areas only for point patterns that are clustered, but as many as 2,000 relocations are required before one can detect a difference between a random and clustered point pattern (Bingham and Noon, 1997). Finally, the method proposed by Kenward et al. (2001) has no way of differentiating between random and clustered space use patterns and might define core areas that do not exist due to the inherent limitations of cluster analysis (James and McCulloch, 1990).

A recent report claims that the estimation of core areas has been relatively well studied (Laver and Kelly, 2008). While it is true that many studies have discussed new methods and problems associated with estimating core areas, no consensus exists, and many of the problems inherent in the current methods continue to remain unaddressed. Any method used to estimate core areas should have the following traits: 1) it can be used across home range estimation techniques, 2) is founded on the definition of a core area (i.e., clustered point patterns), 3) only identifies core areas when they exist, 4) is capable of delineating multiple core areas within a home range, and 5) is dependent on individual data sets and not arbitrary rules. Another ideal trait of a core area estimation method would be an ability to assess the degree of uncertainty surrounding a core area estimate. Certainly we will never produce an estimate of a core area boundary that is perfect, and it is likely that there does not exist a hard boundary which defines the core area. We are unaware of any core area delineation method that addresses the above five characteristics in addition to formally accounting for uncertainty regarding the core area estimate.

In what follows, we draw on well-established methods in spatial statistics to present a novel approach to delineating core areas that is non-arbitrary and based on a clear definition and set of conditions regarding core areas.

2. Material and Methods

2.1 Definition and Fundamentals

We begin by providing a formal definition of the core area along with a set of fundamental conditions that are useful for specifying a statistical model that characterizes the core area based on the given data set. As such, consider the following conditions:

1. There exists a home range, represented by a subset of \mathbb{R}^2 , the boundary of which can be defined by \mathcal{H} .
2. There exists a random subset of \mathcal{H} that denotes the core area \mathcal{C} .
3. For any realization of the core area, \mathcal{C}_* , \mathcal{H} can be partitioned into two disjoint sets: $\mathcal{H} = \mathcal{C}_* \cup \mathcal{C}'_*$ (where, the $'$ indicates a set complement).
4. A temporally independent observed point process, \mathcal{X} , in \mathcal{H} , is doubly CSR; that is, independently CSR in both \mathcal{C} and \mathcal{C}' (where CSR is short for complete spatial random, or 2-D uniform).
5. Isopleths of a kernel density estimate on \mathcal{X} can well approximate \mathcal{C}_* .
6. We seek to characterize \mathcal{C} using \mathcal{X} .

Using the above conditions and a set of data \mathcal{X} meeting the criteria, we seek to find an optimal stochastic partition of the home range \mathcal{H} such that the realization of animal space use (\mathcal{X}) is CSR on two disjoint spatial domains, \mathcal{C} and \mathcal{C}' .

Casually, based on our definition of the core area, we are assuming that the observed animals will behave in such a manner that they occupy regions of their home range (\mathcal{H}) with differing intensities. We do not attempt to discern whether the apparent aggregation of observed animal locations in most data sets arises due to first order or second order spatial effects. Rather, when significant clustering is indicated in a given data set (as determined through a formal hypothesis test using the L-function), we assume that the aforementioned partition of \mathcal{H} exists and the data \mathcal{X} are actually two separate point processes with two separate spatial domains. Additionally, we assume that the animals use each of the spaces in a complete spatial random fashion and that the partition is random rather than fixed. This latter assumption can be intuitively justified by considering that the animal is likely unaware of some fixed polygon in its home range that denotes “core” space use. Though fairly hard boundaries may exist as landscape features (e.g., water bodies, topographic conditions such as ravines or cliffs, forest edge), we still feel that the core area should be flexible enough to accommodate variability in the boundary. Allowing \mathcal{C} to be defined as a random subset of \mathcal{H} is a reasonable way to allow for uncertainty in the boundary if it is necessary, while it is also capable of being precise if the data suggest that it should be. Alternatively, this problem could be thought of as a binary marked point process, where the marks of the observed point process \mathcal{X} correspond to the those points inside and outside the core area \mathcal{C} . Though we do not set up the problem in this manner, inference resulting from our approach allows us to learn about these unknown marks.

In the next sections we will discuss the manner in which the data (\mathcal{X}) are collected and then develop a model suitable for finding the optimal partition \mathcal{C} for the situations where it is reasonable to use the doubly CSR definition of a core area.

2.2 Data

One of the most common forms of spatial point process data for animal locations arises from radio telemetry studies where the animal of interest is collared with a transmitter and can be located at desired future times using a receiver and antenna. Depending on the study and the species of interest, measures can be taken to ensure that observations of animal locations are temporally independent. Thus, any inhomogeneity in observed animal locations will arise due to spatial effects (either first or second order) and not because of latent temporal autocorrelation.

In application of the methods presented here, we consider the following data sets on three individual animals (Figure 1) that have the properties discussed above. We also use simulated data to examine the effectiveness of the methodology, though these results are not provided here due to space limitations.

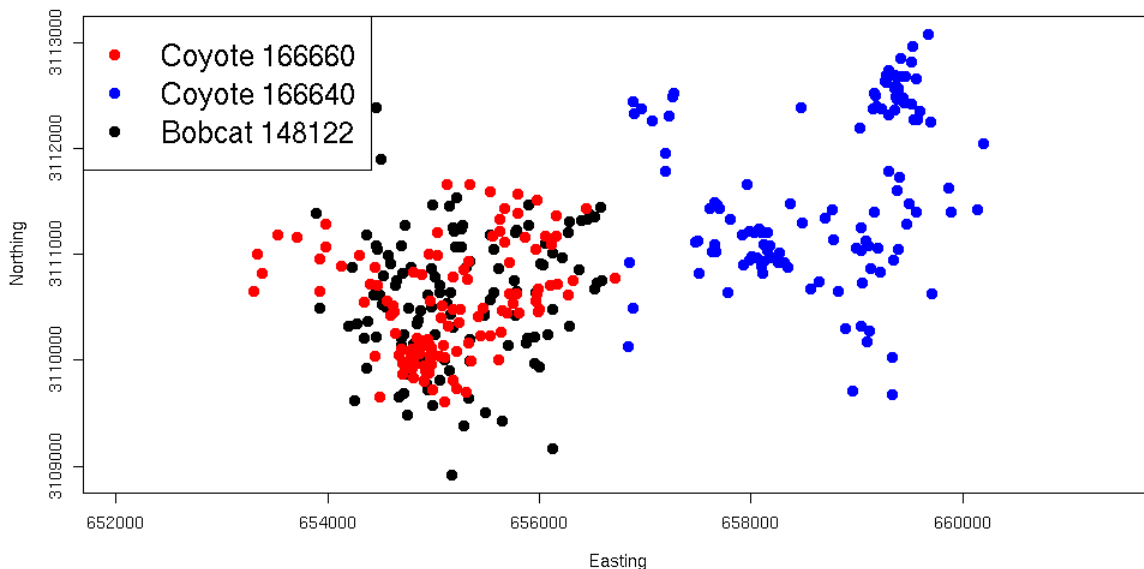


Figure 1: Temporally independent radio telemetry spatial point process data assumed to represent animal space use.

Note that several different patterns arise in the observed spatial point processes shown in Figure 1. For example, the two coyotes (animals 166640 and 166660, red and blue dots) appear to indicate clustering, though one exhibits two distinct core usage areas while the other only exhibits one. The bobcat (animal 148122, black dots), on the

other hand, still indicates a clustered pattern but over a much larger area.

2.3 Core Area Model

In the development of a statistical model, we rely directly on our definition of the core area as previously presented (i.e., partitioned double CSR point process). This implies that the observed set of spatial locations should arise from two independent uniform probability distributions with irregular boundaries. The support in such a model is troublesome for inverse modeling as it complicates the tractability of statistical distributions. That is, since we seek to find the optimal stochastic partition \mathcal{C} such that $\mathcal{X}(\mathcal{C}) \sim \text{CSR}(\mathcal{C})$ and $\mathcal{X}(\mathcal{C}') \sim \text{CSR}(\mathcal{C}')$, the distribution of an estimate of \mathcal{C} is impossible to find given our definition of a core area and assumptions. Additionally, due to the model we have specified, it is difficult to evaluate a uniform likelihood when the observed data are not independent on the support. That is, without a knowledge of the correct support (i.e., \mathcal{C} and \mathcal{C}') we cannot easily evaluate a joint uniform density at $\mathcal{X}(\mathcal{C})$ and $\mathcal{X}(\mathcal{C}')$ without accounting for potential dependence in the data.

Thus for a data model (i.e., likelihood), we use a spatial transformation of the data and specify a discrete likelihood that will be approximate but still representative of our core area definition.

2.3.1 Data Transformation

We first transform the data so that it has discrete spatial support rather than continuous spatial support over \mathcal{H} . By dividing the home range (\mathcal{H}) into a finite number (say m) of square grid cells or bins, and then counting the number of observed animal locations that fall within each in bin, we will end up with an m dimensional set of counts, \mathbf{N} . These counts, $\mathbf{N} = \{N_1, \dots, N_i, \dots, N_m\}$ now represent the number of observed points in each region of the home range.

2.3.2 Approximate Likelihood

Now, assuming our double CSR model for the core area and conditioning on a core area \mathcal{C} , we can partition \mathbf{N} into the core bin counts $\mathbf{N}(\mathcal{C})$ and the non-core bin counts $\mathbf{N}(\mathcal{C}')$. If the corresponding animal locations (\mathcal{X}) are CSR in \mathcal{C} and \mathcal{C}' , then we expect the sets of counts to have multinomial distributions with equal multinomial cell probabilities (i.e., $\mathbf{p}_{\mathcal{C}}$ and $\mathbf{p}_{\mathcal{C}'}$). If we let $n_{\mathcal{C}}$ and $n_{\mathcal{C}'}$ denote the total number of points inside and outside the core area, respectively, then we have the following likelihood:

$$\mathbf{N}|\mathcal{C} \sim \text{MN}(n_{\mathcal{C}}, \mathbf{p}_{\mathcal{C}}) \times \text{MN}(n_{\mathcal{C}'}, \mathbf{p}_{\mathcal{C}'}) . \quad (1)$$

In practice, there will be an edge effect due to the fact we are not partitioning the space of \mathcal{H} with perfect precision, however if the number of bins is large enough, this edge effect will be minimal.

2.3.3 Model for \mathcal{C}

Specifying an appropriate model for the core area boundary \mathcal{C} is perhaps the most challenging component of the methods we present here, because, if left unconstrained, \mathcal{C} would require an infinite dimensional parameter space. Thus, we will assume the boundary itself can be well-modeled by an isopleth (i.e., level line) of a kernel estimate of the density of the observed point process \mathcal{X} . There are, of course, other methods for delineating polygons (e.g., the convex hull, wombling), however since kernel density estimation (KDE) is frequently used in animal space use studies and we have used it for delineating the home range boundary in this study, we will continue to employ it here. Advantages are that it is well studied and there exist various preferred methods for choosing appropriate bandwidth values depending on the situation at hand. In fitting an inverse model, the KDE isopleth (ϕ) is especially attractive because it is bounded between zero and one and we can treat it as a statistical parameter to estimate. Once estimated, ϕ completely determines the core area partition \mathcal{C} . Thus, the likelihood from (1) can be conditioned on ϕ rather than \mathcal{C} . This results in a much more parsimonious model parameterization and is quite computationally tractable.

2.3.4 \mathcal{C} Hard or Soft?

As discussed in the Introduction, we believe that the core area itself is cannot be adequately represented by a single polygon (or polygons) in space, but rather should be more realistically considered as a random set within the home range \mathcal{H} . Additionally, due to the fact that we are substantially constraining an estimate of \mathcal{C} by assuming it is well-modeled by a KDE isopleth, we feel it is responsible to allow the core area, now represented by ϕ , to be random and its distribution is then what we wish to estimate.

A statistical model can be easily constructed using Bayesian methods that incorporate the likelihood (1) and any prior knowledge about the isopleth parameter ϕ . For example, well studied species may have already provided scientists with a good understanding of the size of typical core areas for those animals and this information could be used in a subjective prior distribution on ϕ . Here, we will only assume that ϕ should not be too near zero nor too near one, thus we specify a relatively vague beta distribution as a model for ϕ with hyperpriors both equal to 1.1 and 1.1.

2.3.5 Implementation

The model described above is relatively simple to implement as a one-parameter Bayesian model and although there is non-conjugacy induced through the nonlinearity of the ϕ parameter in the likelihood, this can be overcome using an accept-reject style algorithm such as Metropolis-Hastings (Gelman et al., 2004). In doing so, we seek to find the posterior distribution for the isopleth parameter ϕ given the multinomial count data \mathbf{N} :

$$[\phi|\mathbf{N}] \propto \text{MN}(\mathbf{N}_C | n_C, \mathbf{p}_C, \phi) \times \text{MN}(\mathbf{N}_{C'} | n_{C'}, \mathbf{p}_{C'}, \phi) \times \text{Beta}(\phi|1.1, 1.1) , \quad (2)$$

where, the square bracket notation refers to a conditional probability distribution. Since we assume that ϕ completely determines \mathcal{C} , this will also yield a random shape that delineates the posterior core area.

3. Results

First, we delineate the home range using the 95% isopleth of a kernel density surface based on the observed data with a default bandwidth. This is a commonly used definition of the home range and we have found that it works well for the situations we present here, though other methods could be used as an alternative. Using the data shown in Figure 1, we then ascertained whether it is reasonable to try to estimate a core area for each of the animals under study by using the L-function to assess if clustering is apparent in the data. Finally, we fit the core area model a total of three times, one for each of the animals under study. The results of these main steps are presented in the following sections.

3.1 Exploratory Clustering Analysis

If there were no clustering evident in the observed spatial point processes (Figure 1) we would not expect to be able to estimate a core area given our definition and model assumptions. Thus, as part of an exploratory analysis we estimated the L-function in each of three situations (Figure 2) to see if there appeared to be departure from CSR at any particular spatial lags.

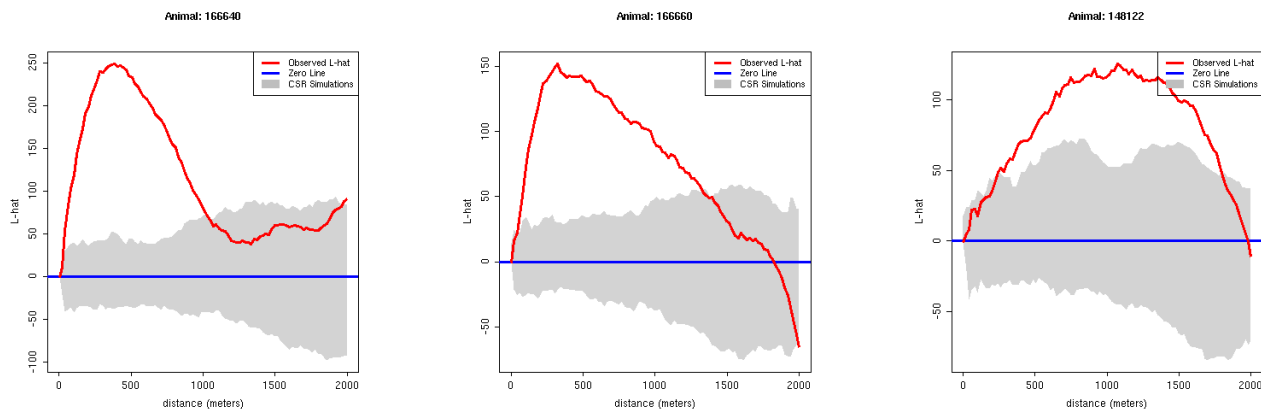


Figure 2: Estimated L-functions for each of the observed spatial point processes shown in Figure 1. Note that each indicates significant clustering at some spatial lags between 0 and 2000 (meters) due to its departure from the CSR envelopes.

3.2 Core Area Modeling

Using the delineated home range mentioned above, a regular grid was chosen for each spatial domain on which the data transformation (binning) was performed in order to obtain the multinomial count vectors \mathbf{N} for each of the

animals in Figure 1. Each of the core area models were then fit to the multinomial data using 5,000 Metropolis-Hastings samples and relatively vague priors on ϕ , as discussed in the Methods section. The Metropolis-Hastings algorithm requires a starting value for the isopleth parameter ϕ which was chosen based on the isopleth closest to representing the maximum distance at which clustering occurs (Figure 2) for each of the data sets. Each of the model runs were tuned visually such that the Markov chains mixed well and yielded an acceptance rate near 30% (close to optimal for quasi-Gaussian posterior distributions). By visually analyzing the Metropolis-Hastings samples, We found that convergence to the stationary posterior distribution occurred rapidly and thus a burn-in of 500 samples were removed from the chain before calculation of posterior statistics.

The estimated posterior distributions for the isopleth parameter ϕ are shown in Figure 3, while the corresponding posterior core area sizes (in hectares) are compared in Figure 4. These posterior distributions can be used to display the core area spatially in relation to the data and home ranges (Figure 5). As mentioned earlier, the problem we are addressing with this core area model could also be thought of in terms of classification. That is, researchers might wish to make inference about the posterior membership of observed animal locations to either the core area (\mathcal{C}) or non-core area (\mathcal{C}') within the home range. In this latter set of plots (Figure 5), we present this posterior information in terms of probability of membership for each point in the data set.

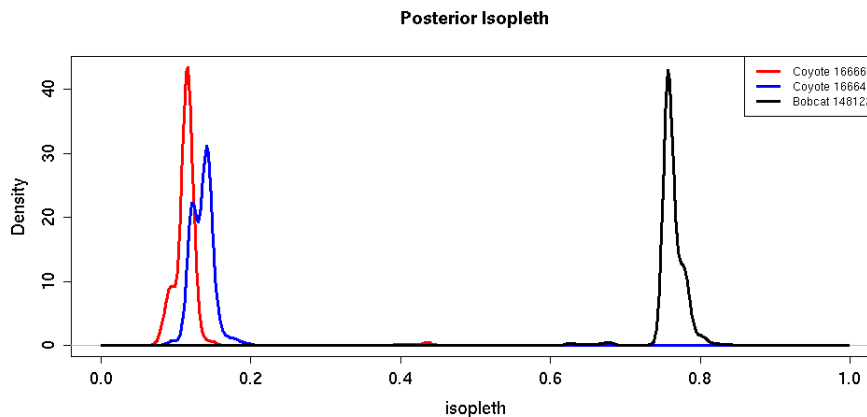


Figure 3: Posterior distributions for the isopleth parameter ϕ using each of the animal location data sets.

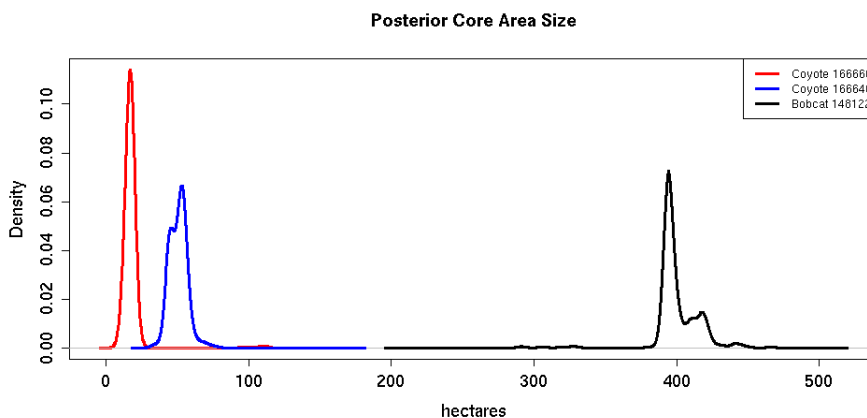


Figure 4: Posterior distributions for the core area sizes in hectares using each of the animal location data sets.

4. Discussion

Based on the exploratory clustering analysis of each set of observed animal locations (Figure 2), we have reason to believe that each of the animals under study exhibits some degree of spatial clustering over their home range, though at different spatial scales. Visually, it is easy to verify this result and we can see that each of the coyotes (Figure 1) appear to have much smaller clusters in their complete data sets than the bobcat, however coyote 166640 indicates

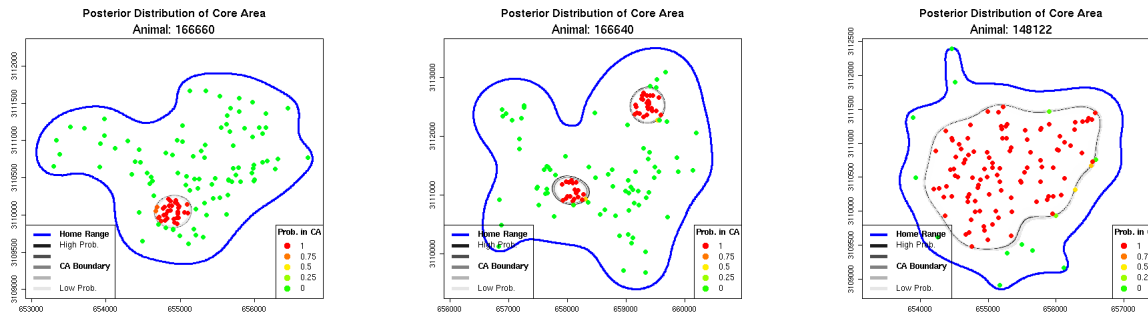


Figure 5: Posterior core areas and posterior membership probabilities for observed animal locations. Note that the entire posterior distribution of each core area is plotted and shown as a shaded polygon(s). Areas with darker color correspond to more likely core area delineations.

that it may have two distinct cores (or a core area made up of two distinct polygons). This preliminary analysis suggests that there is sufficient reason to continue with the core area estimation procedure by fitting our proposed model to each of the sets of observed animal locations.

Upon fitting each of the models as described in the Results section, we find that indeed the posterior distributions for the isopleth parameter (ϕ) are similar for the two coyotes and those are both significantly smaller than that of the bobcat (Figure 3). The interpretation is slightly different however when viewing the posterior results in terms of the size of the core area in hectares (Figure 4) where we see significantly different (i.e., non-overlapping posterior distributions) core area sizes between all animals in this study. A biologically relevant feature of these results is that, though the general trend of coyote core areas being smaller than the bobcat core area remains, there now exists differences among the coyotes in this study. This could potentially be due to the fact that coyote 166640 is female while coyote 166660 is male and has the larger core area, though more data are needed to see if this finding is true in general, using these methods. We also compared the posterior core area size in proportion to the overall home range size between animals (not shown here due to space limitations) and found a similar relationship to that shown in Figure 3. This might imply that male coyotes simply use more space than female coyotes, while the nature of the core area itself remains fairly constant between the sexes; though again, more data is needed to verify this finding.

The spatial depiction of the posterior core areas in Figure 5 confirms what we were seeing in the exploratory analysis regarding the overall clustering in the full data sets. That is, beyond the difference in posterior isopleths and core area sizes, coyote 166640 has two distinct random polygons that delineate its core area while coyote 166660 has only one. Additionally, we can see that the bobcat (i.e., animal 148122) has a much larger core area, in terms of density isopleth, size, and proportion to home range. Notice also, that in each of the situations, there are a few observed locations that fall neither clearly in core area nor in the non-core area of the home range (as indicated by the membership probabilities near one half; Figure 5), though most fall distinctly in one or the other of the regions. This lends supporting evidence to debunk the notion that a clear fixed but unknown polygon (or polygons) exists that delineates the core area, and thus, perhaps it is more reasonable to think about animal core areas as random subsets of the home range.

Through extensive simulations (results not presented here due to space limitations) we have found that these methods perform quite well for characterizing core areas of arbitrary size and shape, in that, posterior distributions for the core areas regularly overlapped at least 75% of the core boundary used to simulate the data. In terms of sensitivity, we found that the bandwidth used in the kernel density estimation can affect the results, though the general scientific inference often remained the same. In that, the posterior core area shape would become more complex with a decreased bandwidth but the core area size and proportion to the home range varied little. Also, with regards to sensitivity, we found the model to be fairly robust to changes in the number of multinomial bins used (m); however, as one might expect, we did notice that a larger number of bins was needed for data sets with larger numbers of observed animal locations.

5. Conclusion

In summary, we have presented a non-arbitrary, data-based method for statistically characterizing animal core areas based on the simple definition that if it exists, a core area should consist of two disjoint random sets of the animal home range wherein the observed animal locations should arise as two independent CSR processes. We have found this method works well with simulated data and provides valuable scientific insight on the space use of various

animals. Our method, though perhaps non-trivial in its implementation, is intuitive in principle and uses techniques familiar to wildlife researchers (e.g., kernel density estimation). Additionally, it could be readily generalized to other situations (e.g., epidemiology or military applications) or be augmented to use numerous datasets simultaneously to account for variability among individuals and various classes of animals (e.g., sex or age) while make inference about the population as a whole or between populations or species.

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